

Integrating statewide research and monitoring data for mule deer in Montana



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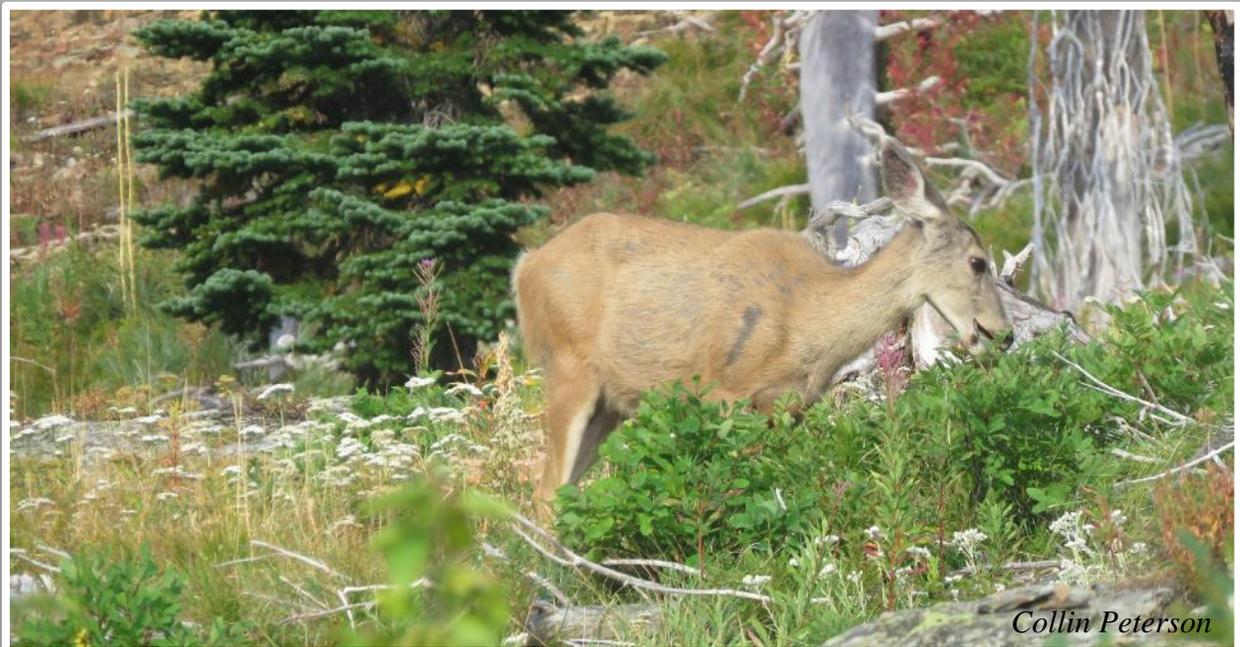
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**MONTANA FISH,
WILDLIFE & PARKS**



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Background and summary

Over the past century, mule deer (*Odocoileus hemionus*) have experienced periods of population growth and decline throughout their range (Mackie et al. 1998, Pierce et al. 2012, Bergman et al. 2015). Studies of mule deer population dynamics have revealed a suite of interacting factors which influence annual variation and trends in population growth (Mackie et al. 1998, Unsworth et al. 1999, Pierce et al. 2012, Monteith et al. 2014, Hurley et al. 2014, Ciuti et al. 2015). The complexity of mule deer population dynamics creates a challenge for biologists seeking to monitor local deer populations and respond with appropriate management decisions in a timely manner (White and Bartmann 1998, Bishop et al. 2005).

Mule deer population trends are of particular concern in Montana, where significant declines in abundance and hunter harvest (correlated) have been documented in many areas throughout the state. Wildlife managers are tasked with the difficult mission of maintaining or recovering deer populations, dampening the magnitude of potential future declines, and stabilizing populations and subsequent hunter opportunity. Therefore, improved quantitative understanding of mule deer dynamics is of relevance across Montana. The methods by which Montana Fish, Wildlife and Parks (MFWP) currently monitors and manages mule deer were established in 2001 with the adoption of the Adaptive Harvest Management (AHM) system (MFWP 2001). This system included four primary components: 1) population objectives, 2) monitoring program, 3) hunting regulation alternatives, and 4) population modeling. The population modeling component of AHM was initially designed to predict future deer dynamics given a suite of harvest and weather scenarios. Despite being founded upon very powerful data sets, Pac and Stewart (2007) found the AHM population models achieved mixed results and subsequently recommended they remain in an experimental phase rather than be implemented as a management tool.

MFWP currently collects multiple sources of monitoring data to guide management decisions under the AHM system, and distinct from this current process are other vital rate data collected as part of research studies. With this project, we seek to leverage existing monitoring and research data together for an integrated quantitative assessment of mule deer dynamics for guiding management. Additionally, we aim to collect novel field data in portions of northwest Montana and along the Rocky Mountain Front where biologists are faced with reduced mule deer numbers yet lack basic ecological and population information to manage with strong confidence.

Location

Field studies are focused in Lincoln, Flathead, and Lewis and Clark counties, where mule deer use 3 different and less understood habitat types. Population modeling involves utilization of research and monitoring mule deer data from across their statewide distribution.

Study Objectives (2019-2020)

During the 2020 fiscal year, we continued work towards 4 primary objectives:

- 1) Integrated population modeling: build and evaluate integrated population model for one of Montana's seven administrative regions: Region 7, southeastern Montana
- 2) Complete basic field monitoring of adult female mule deer in 3 study areas
 - a. Vital rate monitoring
 - b. Space use and migration
 - c. Diet composition, winter & summer
- 3) Assess mule deer summer habitat selection
 - a. Vegetation sampling & forage modeling
 - b. Risk-forage trade-offs
 - c. Relationships to landscape disturbance
- 4) Assess mule deer winter habitat selection

Objective #1: *Integrated population modelling*

Integrated population models (IPMs) are growing in use by management agencies seeking to accommodate multiple data streams that characterize populations (Cooper et al. 2003, Schaub et al. 2007, Johnson et al. 2010, McCaffery and Lukacs 2016). One advantage of this approach is that it aligns multiple data streams into a single model of the population, while weighting the contribution of each data set according to its relative precision. A second advantage is that it formalizes the level of uncertainty surrounding any given point estimate, such that estimates of population trend or recruitment ratios come with explicit attention to precision. Third, one can incorporate links to environmental covariates into population models, which show particular potential for mule deer given links between remotely-sensed metrics of climate and vegetation and concurrent deer population dynamics (Mackie et al. 1998, Hurley et al. 2014, Ciuti et al. 2015, Stoner et al. 2016). Lastly, these models could conceivably facilitate the extrapolation of patterns from data-rich portions of the state to those without comparable monitoring data.

Our mule deer IPM will begin with a simple mathematical construction of annual mule deer dynamics, requiring input data for animal abundance and vital rates. Models can initially be informed by prior values derived from the literature, and then the fit adjusted according to input data from local populations. For example, Hurley et al. (2017) presented models that predicted 70-80% of the variation in over-winter fawn survival with 3 weather covariates (% snow cover winter, weeks of snow cover in Nov/Dec, and fall plant productivity). Applying such models to weather data across various management units in Montana may be one means to set meaningful prior values in an IPM framework.

During FY20, David Messmer, FWP, has been leading the continued development of population models, focused initially in Region 7 of southeastern Montana. IPMs are founded upon a basic biological model of population dynamics according to groups of animals in different age- and sex-classes, and the corresponding rates at which they survive and reproduce. An observation model is then used to fit available data to that model. In our case, the population model delineates fawns from adults (≥ 1.5 year-olds) for both sexes (Figure 1). Observation data

including trend area counts as well as age- and sex-composition data are used to inform these population segments, and then change over time in these parameters yield informative information for estimating vital rates regarding survival and recruitment (Figure 1). Survey data are founded upon trend areas, which represent a subset of the area over which hunting districts span. Thus, there is somewhat of a disconnect between the populations being sampled with survey vs. harvest data. For this reason, we are currently exploring the use of harvest data as a covariate for informing survival rates rather than removing harvest totals from the population abundance itself (Figure 1). This leaves us currently modelling “relative abundance” of animals within trend areas without adjusting to total hunting district population size, thus far.

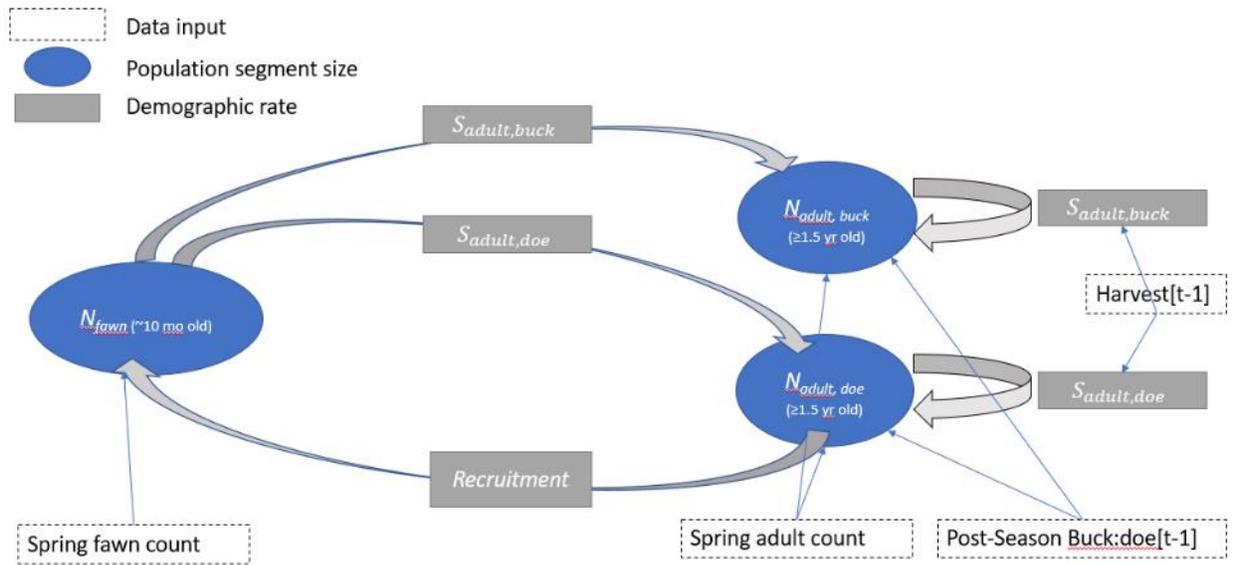


Figure 1. Conceptual model of both the population model, derived demographic rates, and data inputs for modeling mule deer dynamics in FWP administrative Region 7 using available survey and harvest data, Montana.

Preliminary results evaluating this model with data from Region 7, 2000–2017 do seem promising. The iterative fitting of the model over many possible values of various demographic rates results in best posterior estimates that are biologically meaningful, without any informative prior information being used to constrain such rates. Below are some plots of model outputs including relative abundance, vital rates, and composition ratios (Figure 2a–c).

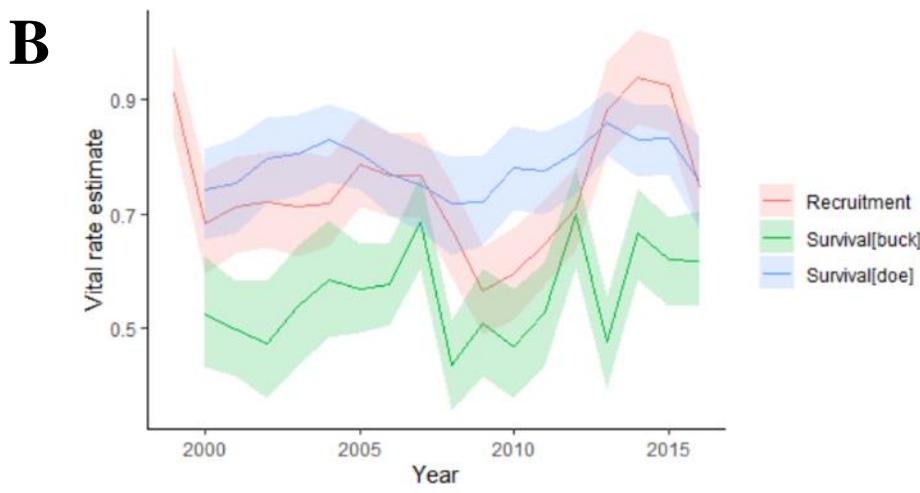
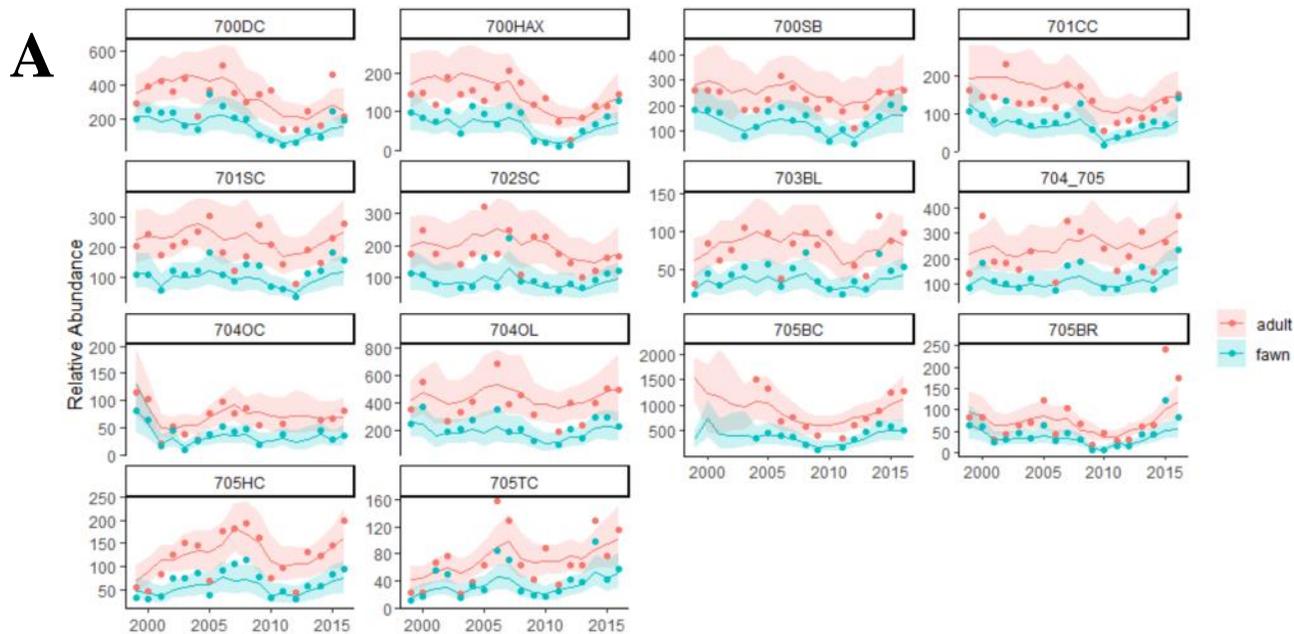
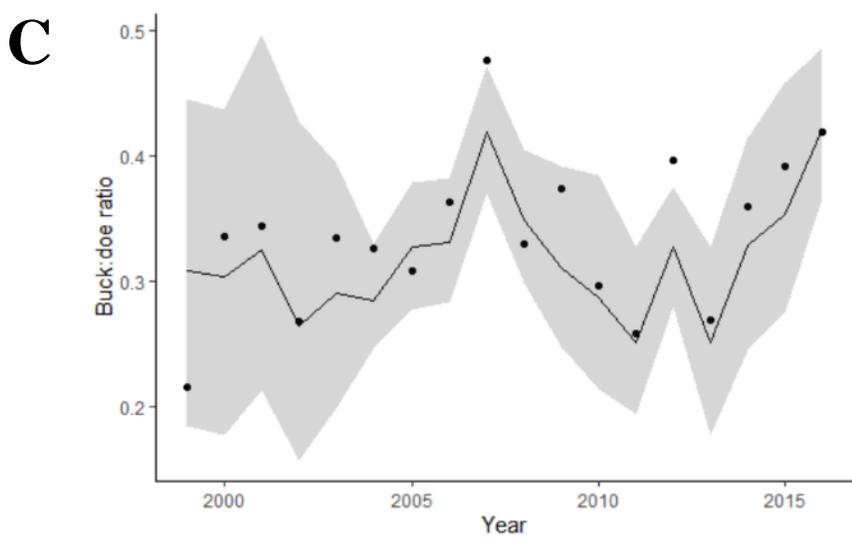


Figure 2. IPM estimates of a) relative abundance by age class and hunting district, b) region-wide vital rates, and c) region-wide buck:doe ratios for mule deer in Region 7 during 1999–2016.



Objective #2: Field monitoring of deer in 3 study areas of Montana

2.1. Vital rate monitoring

Field studies are now completed for monitoring mule deer vital rates, seasonal space use and migration, habitat selection, and summer forage across 3 study areas (Figure 3). In total, we captured and radio-collared 134 adult female mule deer for these purposes using a combination of helicopter net-gunning (Table 1).

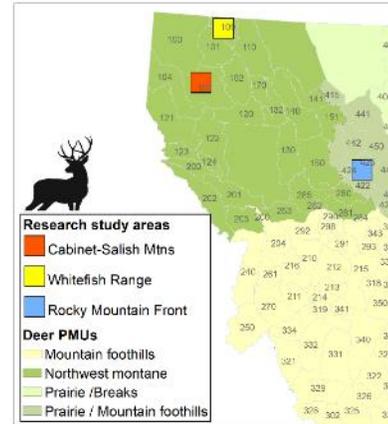


Figure 3. Mule deer field research study area locations, 2017-2020.

Table 1. Numbers of adult female mule deer captured and radio-collared across 3 study areas, 3 winter seasons, and 3 capture techniques, Montana, 2017–2019.

	<u>Rocky Mtn Front</u>		<u>Cabinet-Salish</u>		<u>Whitefish Range</u>	
	Helicopter net-gun	Ground darting	Helicopter net-gun	Clover trap	Helicopter net-gun	Clover trap
2017	28	1	0	0	2	0
2018	12	0	16	10	0	29
2019	8	0	0	15	0	13
Total	49		41		44	

Pregnancy rates were high in all 3 study areas, though a higher proportion of yearlings (with reduced pregnancy rates in this age class) was notable in the Cabinet-Salish study area (Table 2).

Table 2. Pregnancy rates by age in 3 study areas, Montana, 2017–2019.

	<u>All females</u> (age ≥ 1.5)		<u>Yearlings</u> (age = 1.5)		<u>Adults</u> (age ≥ 2.5)	
	Pregnancy	<i>n</i>	Pregnancy	<i>N</i>	Pregnancy	<i>n</i>
<i>Cabinet-Salish</i>	81%	31	43%	7	100%	22
<i>Rocky Mtn Front</i>	98%	54	100%	2	98%	48
<i>Whitefish Range</i>	96%	44	82%	11	100%	30
Total	93%	129	70.0%	20	99%	100

Adult female survival estimates and 95% confidence limits were similar and overlapping across all 3 study areas (Figure 4). Mean annual adult female survival was 0.77 (0.72–0.83), and point estimates in each study area were 0.79 (Cabinet-Salish), 0.77 (Rocky Mountain Front), and 0.75 (Whitefish Range). All 3 study areas showed highest rates of mortality occurring in early spring, during April and May (Figure 4).

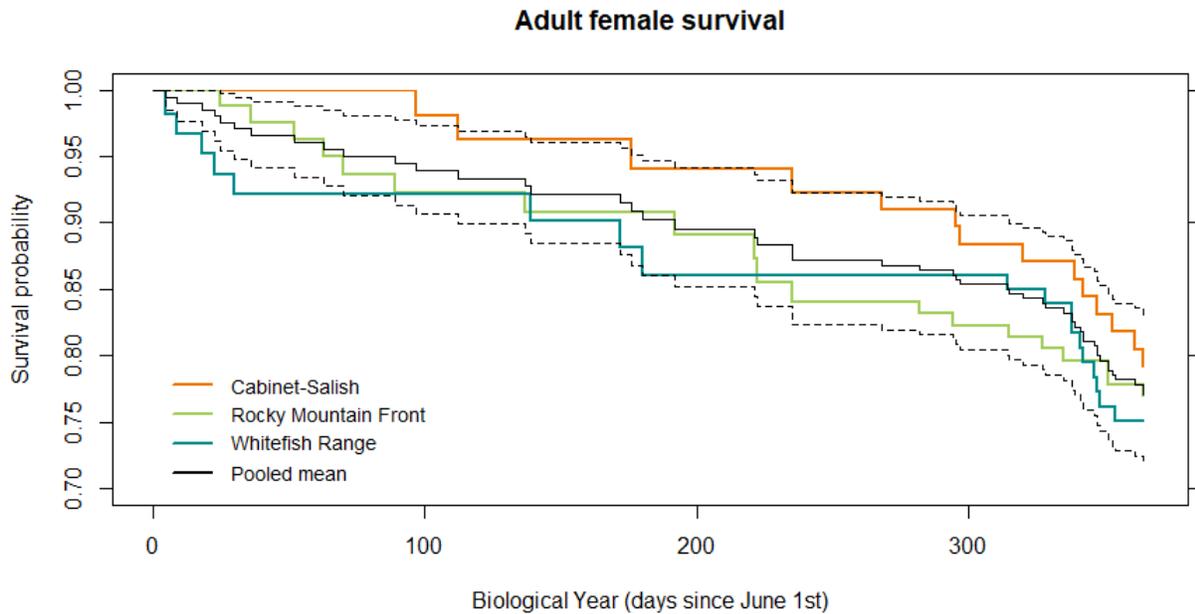


Figure 1. Kaplan-Meier adult female survival estimates for 3 study areas, 2017-2020.

We used a cumulative incidence function estimator developed by Geskus (2011) to estimate cause-specific mortality rates, while accounting for the staggered entry of animals into the data stream throughout the study period. For these estimates we pooled data in the 2 northwestern Montana study areas for comparison with estimates in the Rocky Mountain Front. In all study areas, mountain lion predation was the leading known cause of mortality, imposing 6–11% annual mortality upon adult females across regions (Table 3).

Table 3. Annual, cause-specific, mortality rates for adult female mule deer in 2 regions of Montana, 2017–2020.

	Northwestern Montana (Cabinet-Salish & Whitefish Range) <i>n</i> = 84		Rocky Mountain Front <i>n</i> = 49	
	Estimate	<i>SE</i>	Estimate	<i>SE</i>
<i>Predation, mountain lion</i>	0.11	0.027	0.06	0.028
<i>Predation, wolf</i>	0.01	0.007	0.03	0.017
<i>Predation, coyote</i>	0.01	0.006	--	--
<i>Predation, unknown sp.</i>	0.01	0.011	0.02	0.017
<i>Health-related</i>	0.03	0.013	0.03	0.017
<i>Human (fence entrapment)</i>	0.01	0.008	--	--
<i>Unknown</i>	0.06	0.021	0.09	0.033

2.2. Seasonal space use and migrations

We assessed seasonal space use and migratory behavior using net-squared displacement (NSD) to classify mule deer migration behaviors into either migrant or resident categories (Bunnefeld et al. 2011). NSD measures the straight-line distance between an animal's starting point and subsequent daily locations. We used the R application Migration Mapper (Wyoming Migration Initiative 2019) to view individual mule deer NSD curves to classify their movement behavior. Deer in all 3 study areas exhibited partial-migration behavior whereby some individuals chose to remain resident in a year-round range while others migrate seasonally between spatially distinct ranges (Hebblewhite et al. 2009). We also summarized migration dates (Figure 5) and delineated seasonal home ranges (Figures 6–8). Ongoing work will attempt to assess the triggers of seasonal migration in accordance with anthropogenic and climatic variables.

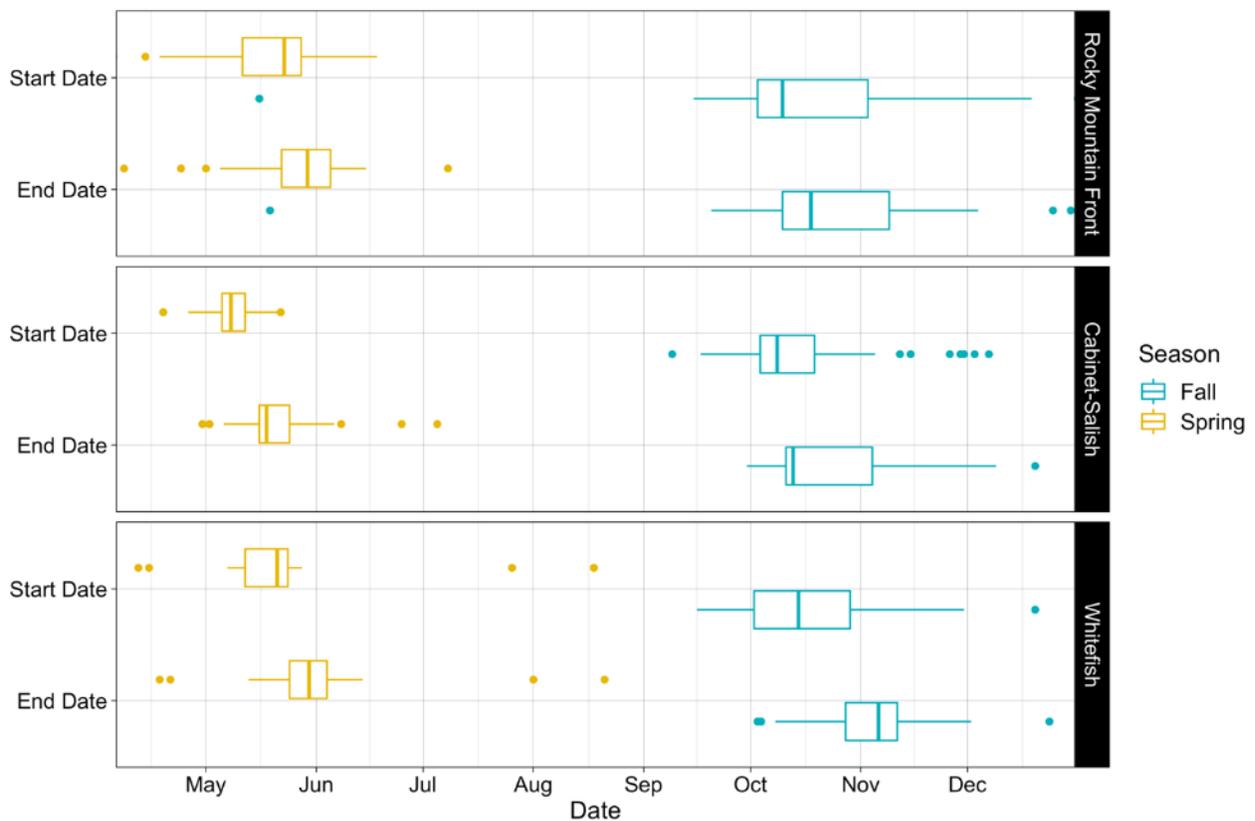


Figure 5. Start and end dates of the migration period during both spring and fall migrations for each of 3 study areas in Montana, 2017–2020.

Rocky Mountain Front

On this study area we were able to assess migratory behavior of 81 unique animal-years from 44 deer. During years 2017-2019, 34 deer were considered migratory, 9 remained residents and 1 utilized both strategies. We documented 66 spring and 45 fall migrations. Mean spring migration distance was 23 km (SD: 14.3, range: 3.1 – 59.5) and mean fall migration distance was 25 km (SD: 13.8, range: 3.9 – 58.1). Across study areas, individuals exhibited strong fidelity to a single strategy from year to year, with the exception of 1 deer on the Rocky Mountain Front that switched behaviors during our study. In 2017, this deer was classified as a resident, but in 2018 she undertook a short distance migration of 9.8 km before returning to her winter range in early summer. Further, in spring of 2017, one deer dispersed 32.4 km southeast to a new home range in plains habitat and remained in this home range when monitoring ended in Fall 2019, so we classified this deer as a resident. Of the deer that migrated, the majority moved westward into the Bob Marshall Wilderness Complex; however, 2 deer migrated southeast along the Rocky Mountain Front and remained in plains habitat yearlong. On average, migratory deer initiated spring migration on May 16 (range: March 10 – June 18) with a mean duration of 10.5 days (SD: 9.7, range: 1 - 68). In fall, deer started migration on November 5 (range: May 16 – December 29) with a mean duration of 9.3 days (SD: 10.9, range: 1 – 60; Figure 5). Individual summer home ranges were larger than those in winter with an average of 43.4 km² (SD: 17.9, range: 27.6 - 103) and 39 km² (SD: 12.7, range: 25.4 – 87.3), respectively (Figure 6).

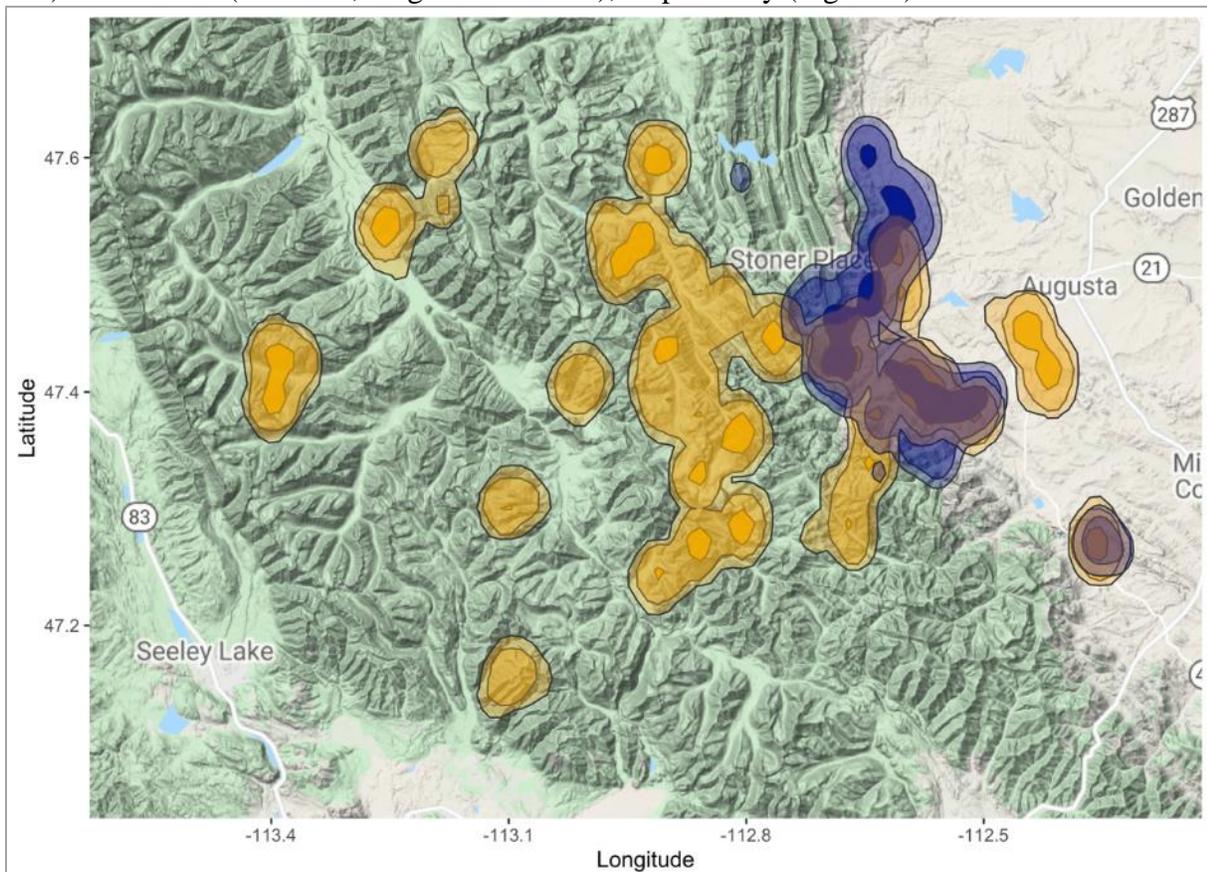


Figure 6. Population scale space use for summer (orange) and winter (blue) for mule deer occupying the Rocky Mountain Front study area.

Cabinet-Salish Mountains

Of the 40 deer collared in the Cabinet/Salish from 2017-2019, we were able to assess migratory behavior of 33 individuals, resulting in 54 unique animal years. We classified 27 deer as migratory and identified 43 spring and 36 fall migrations. Six deer displayed resident space use behavior. Mean migration distance was 33.2 km in spring (SD: 8.1, range: 20.7 – 49.6) and 33.6 km in fall (SD: 7.4, range: 21.4 - 50.1). The direction deer migrated appeared dependent on which side of the Fisher River they over-wintered on. Of the 12 migrant deer collared on the west side of the Fisher, most migrated west and eventually summered in the Cabinet Mountains. Of the 15 migrant deer collared on the east side, most migrated east into the Salish Mountains. On average, deer initiated spring migration on May 7 (range: April 19 – May 22) with a mean duration of 13.3 days (SD: 14.3, range: 1 – 68; Figure 7). In the fall, the average day for initiating migration was October 15 (range: September 9 – December 7) with a mean duration of 7.4 days (SD: 6.7, range: 1 – 34; Figure 5). Overall, summer home ranges were larger than those calculated in winter with an average of 44.1 km² (SD: 18.6, range: 27.4 - 128) and 35.3 km² (SD: 10.6, range: 25.2 – 95.8), respectively (Figure 7).

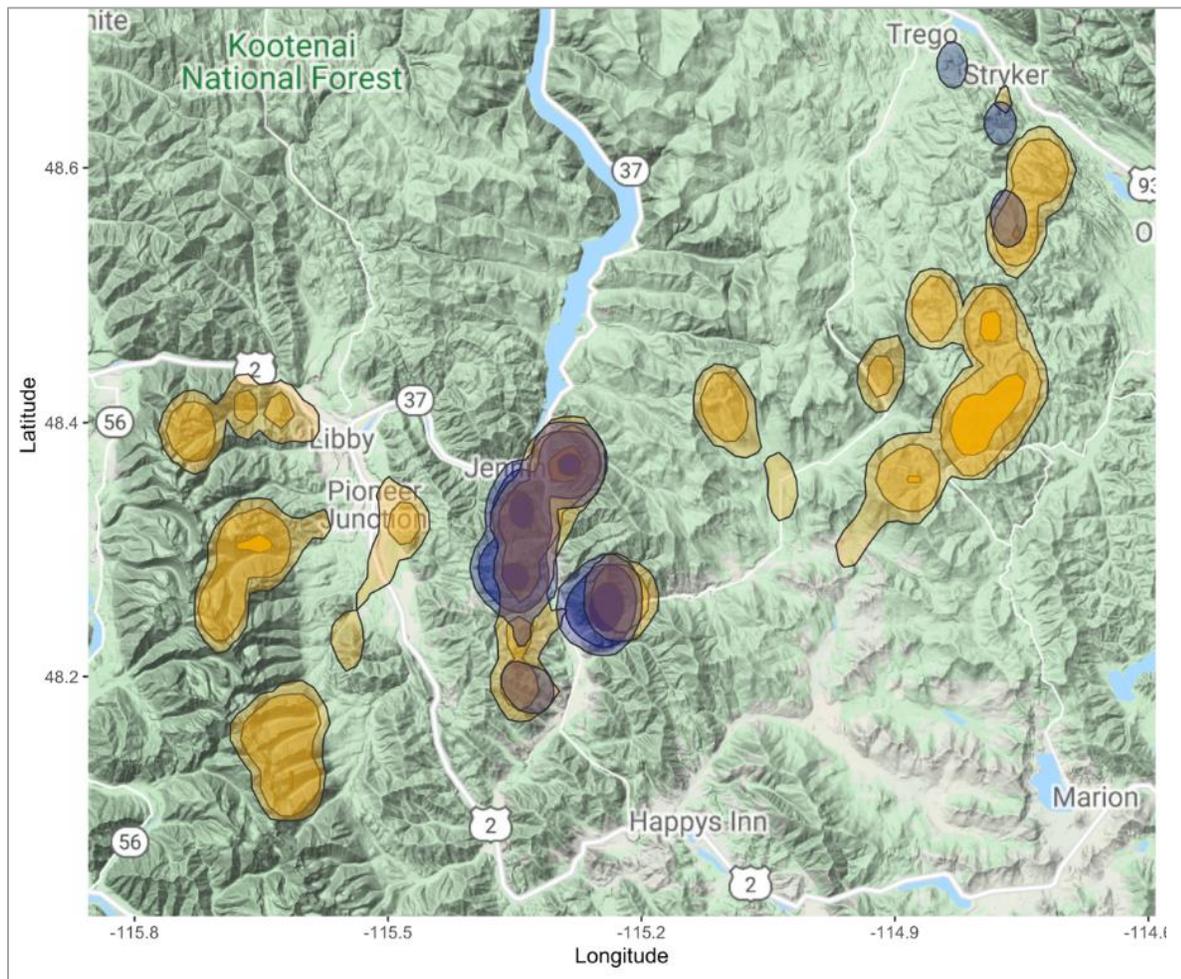


Figure 7. Population scale space use for summer (orange) and winter (blue) for mule deer occupying the Cabinet-Salish Mountains study area.

Whitefish Range

Of the 44 deer collared in the Whitefish range from 2017-2020, 31 deer produced enough GPS locations to assess migratory behavior over 53 unique animal years. Three deer remained residents and 28 deer migrated seasonally, producing 49 spring and 37 fall migrations. Mean migration distance was 23.1 km in spring (SD: 9.7, range: 6.0 – 43.7) and 22.5 km in fall (SD: 10.1, range: 4.1 – 43.8). Four deer crossed the Canadian border and spent their summers in British Columbia, 1 deer spent the summer within Glacier National Park and the majority of the remaining deer migrated east into the Whitefish Range. On average, migratory deer initiated spring migration on May 20 (range: April 12 – August 18) with a mean duration of 10.6 days (SD: 6.7, range: 2 – 23). In the fall, the average day for initiating migration was October 29 (range: September 16 – November 9) with a mean duration of 19.6 days (SD: 17.4, range: 2 – 64; Figure 5). Overall, summer home ranges were larger than those calculated in winter with an average of 49.4 km² (SD: 24.3, range: 25.9 - 121) and 36.3 km², (SD: 17, range: 24.9 - 114) respectively (Figure 8).

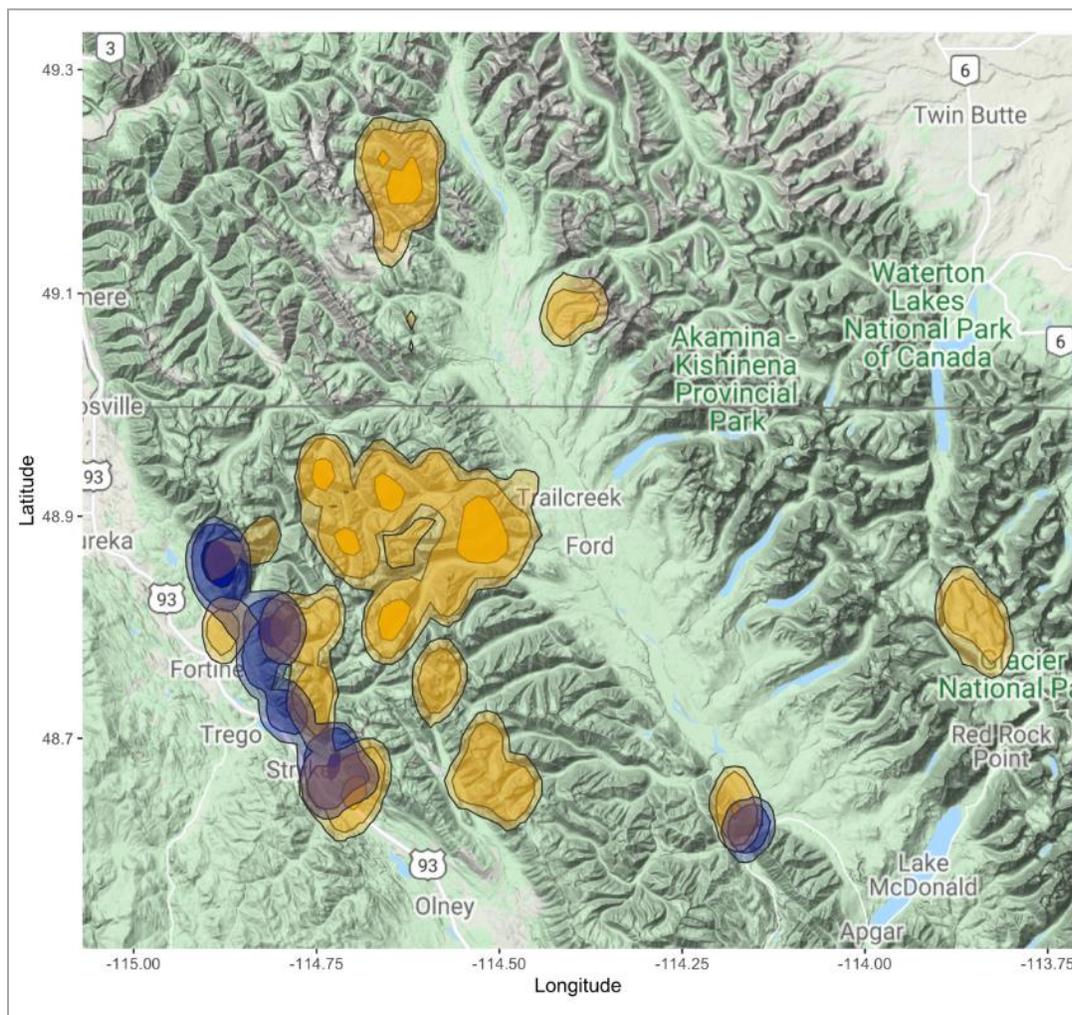


Figure 8. Population scale space use for summer (orange) and winter (blue) for mule deer occupying the Whitefish Mountains study area.

2.3. Diet composition, winter and summer

Diet and nutrition are important drivers of mule deer survival, reproduction and population growth rate (Bishop et al. 2009, Monteith et al. 2014). Therefore, understanding mule deer diet helps to inform population and habitat management. During winter captures, we collected fecal pellets from newly collared mule deer. We directed additional effort during the 2019 summer field season to collect fecal pellets from both collared and un-collared mule deer in all 3 study areas. Through the length of the study, we submitted a total of 99 fecal samples from winter and 104 fecal samples from summer to estimate both individual- and population-level diets across seasons and study areas.

Traditional methods of microhistology assess diet composition based on fecal plant fragments; however, this method can underestimate the importance of forage plants with higher digestibility or faster decomposition (Alipayo et al. 1992). DNA-based approaches isolate a standardized region (DNA barcode) from DNA in fecal samples and compare it to a reference database for identification. The development of next generation sequencing (NGS) can identify up to thousands of species simultaneously (DNA metabarcoding), making DNA-based methods more accessible, faster, and more accurate than ever before (Pompanon et al. 2012). NGS returns the relative quantities of plant species in mule deer diets. Most DNA barcodes matched with an existing plant in the database at 98% similarity. However, some species have nearly identical DNA in a given barcode region, making it difficult to distinguish just one species match from the database. In these cases, we used a hierarchical approach to identify the species, genus, or family with the closest match (up to 95% similarity). To estimate importance of diet species, we calculated the proportion of diet species for individuals and the cumulative proportion for the whole study area (Figures 9, 10).

Summer diets

Due to the close geographic proximity of the Cabinet-Salish and Whitefish study areas, we pooled their diet results to increase sample size. In the Cabinet-Salish and Whitefish Range, shrubs were the most consumed forage class during summer (53% of diet), followed by forbs (39%), and graminoids (8%). On the Rocky Mountain Front, forbs were the most-consumed forage class (57%) followed by shrubs (34%) and graminoids (9%). Across study areas, strawberry (*Fragaria spp.*) was the most consumed diet item during summer, composing 14% of diets in both the Rocky Mountain Front and the Cabinet-Salish and Whitefish Range. Shrubs like *Rubus spp.* and *Rosa spp.* were among the top-consumed species in each study area as well.

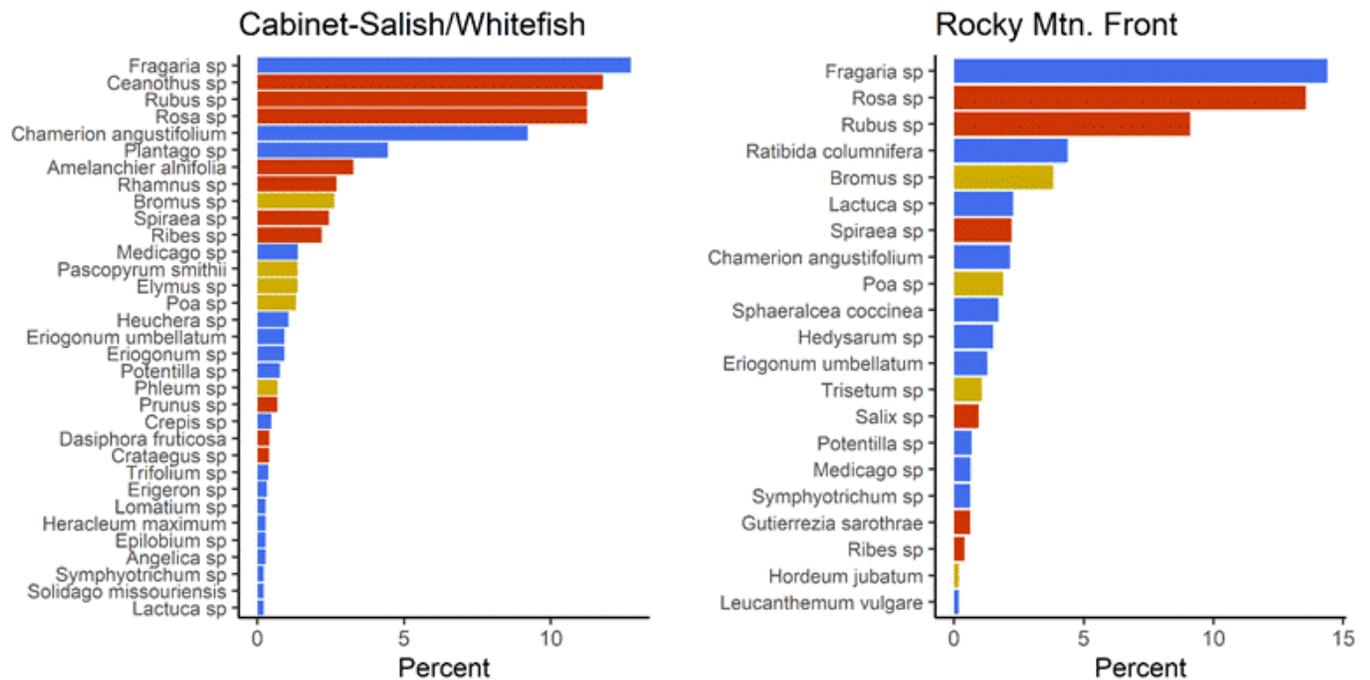


Figure 9. Forage species that make up the top 75% of mule deer summer diets from fecal collections during 2017-2019. Values represent the cumulative proportion of individual diets for a given study area.

Winter diets

Winter diets consisted of more coniferous trees and less forbs than summer diets (Figure 10). In the Cabinet-Salish, shrubs were the most consumed forage class in winter (34% of diet), followed by conifers (26%), graminoids (21%), forbs (19%), and sub-shrubs (<1%). On the Rocky Mountain Front, conifers made up 45% of mule deer winter diets, followed by shrubs (44%), forbs (9%) graminoids (1%), and sub-shrubs (<1%). We classified *Juniperus spp.* as shrubs, not coniferous trees, because that is the growth form that *J. horizontalis* and *J. communis* take on in our study areas. In the Whitefish Range, conifers made up 63% of mule deer winter diets, followed by shrubs (23%), forbs (10%) graminoids (4%), and sub-shrubs and ferns (<1%). Douglas fir (*Pseudotsuga menziesii*) was the most- consumed species in each study area, composing 18%, 30%, and 46% of diets in the Cabinet-Salish, Rocky Mountain Front, and Whitefish Range, respectively.

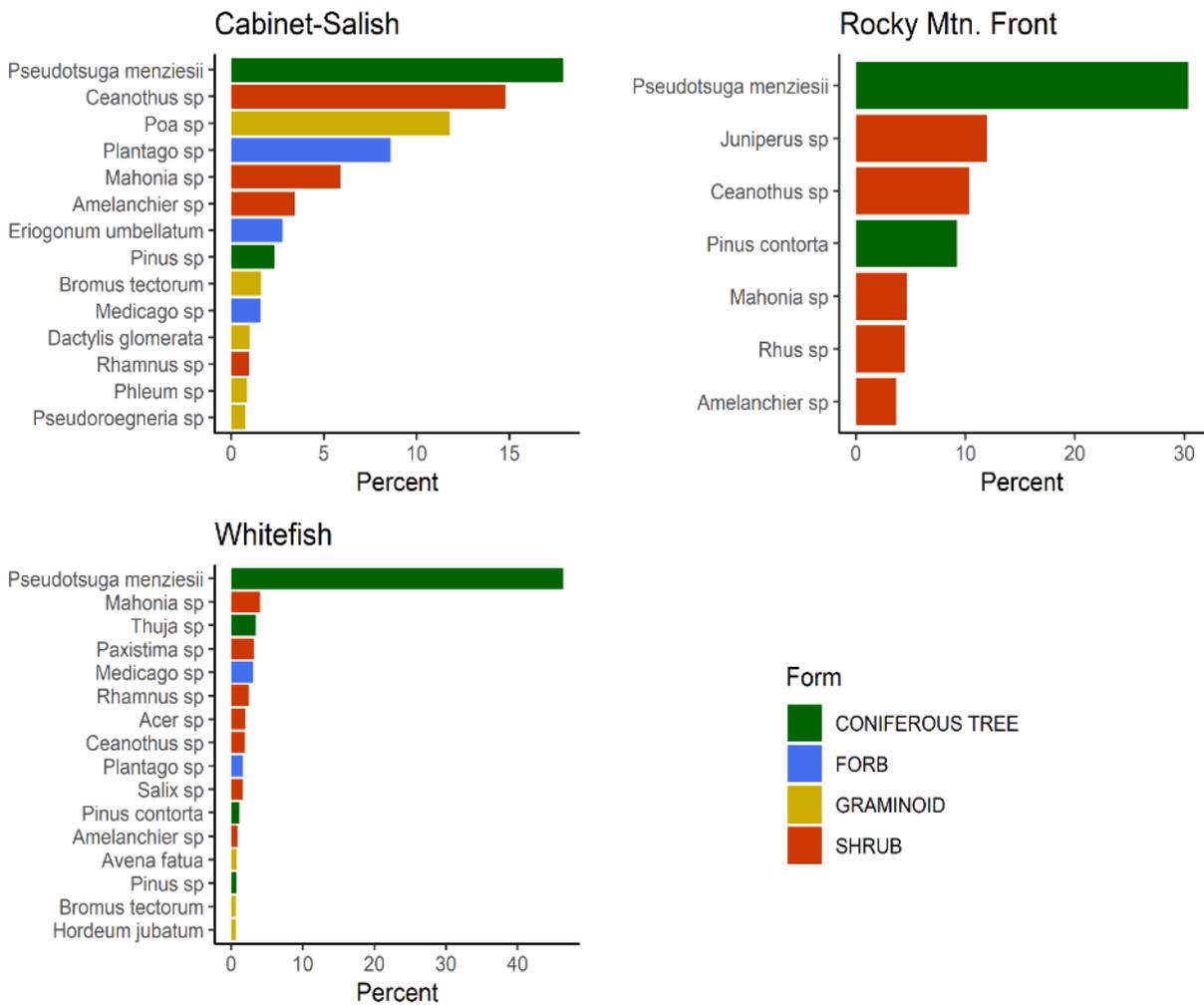


Figure 10. Forage species that make up the top 75% of mule deer winter diets from fecal collections during 2017-2019. Values represent the cumulative proportion of individual diets for a given study area.

Objective #3. Summer mule deer habitat selection and forage studies

3.1 Vegetation sampling and forage modeling

During the summers of 2017, 2018, and 2019, we conducted vegetation surveys and collected fecal samples to characterize mule deer diets and quantify how nutrition is distributed on the landscape. During vegetation surveys, we identified and estimated the cover of all forbs, graminoids, and shrubs in three 1-meter² quadrats. We recorded clipped herbaceous plants and shrubs in a subsection of each quadrat to estimate biomass. Over three field seasons, we surveyed 884 total vegetation plots: 286 in the Rocky Mountain Front, 325 in the Cabinet-Salish Mountains, and 273 in the Whitefish Range. We combined plant composition, biomass, and nutritional data to develop predictive models for estimating forage availability (in kilocalories/m²) during summer, and forage biomass (in grams/m²) during winter (Figure 11).

During summer, in the Cabinet-Salish and Whitefish Range, forage increased with perennial plant cover and southern aspects, and decreased with climatic water deficit, canopy cover, conifer forests, grass/shrublands, and prescribed fires. On the Rocky Mountain Front, forage increased with climatic water deficit, annual plant cover, burns, timber harvests, and moderate slopes, and decreased with canopy cover, perennial plant cover, and low elevation grasslands.

During winter, in Cabinet-Salish we found positive effects of perennial plant cover, wildfires, timber harvests, and grass/shrublands on winter forage biomass, and negative effects of canopy cover. In the Whitefish Range, we found positive effects of grass/shrublands, shrub cover, southern aspects, and moderate slopes, and negative effects of prescribed fires and canopy cover on winter forage biomass. On the Rocky Mountain Front, we found positive effects of perennial plant cover and moderate slopes, and negative effects of conifer forests, shrub cover, and wildfire on forage biomass.

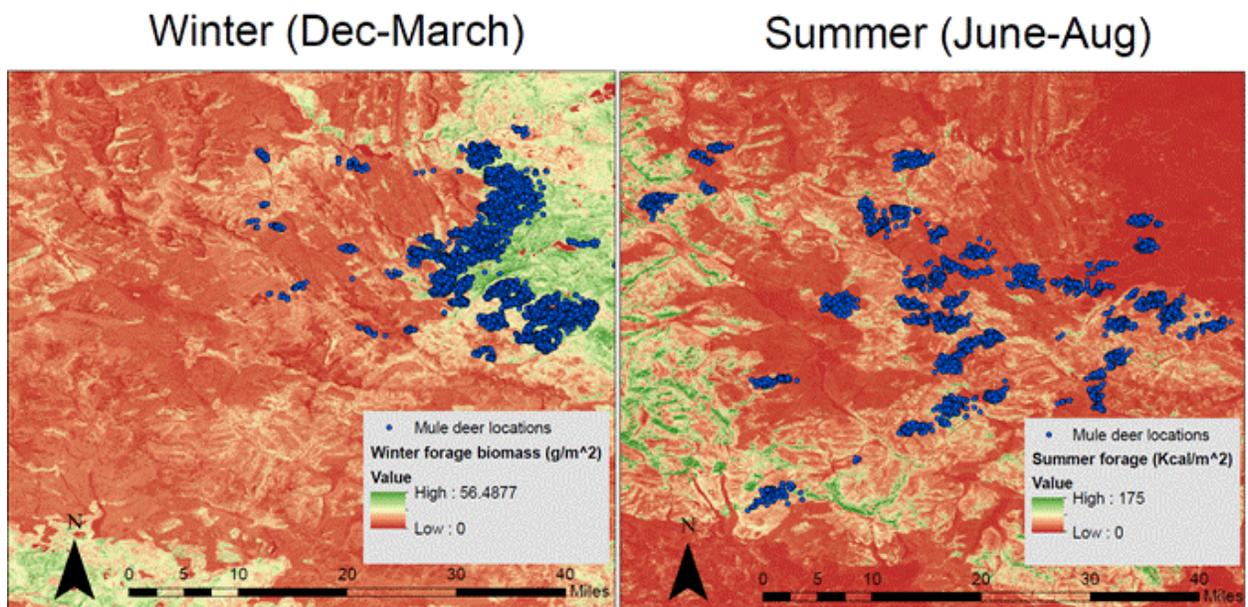


Figure 11. Example of predictive forage models for summer and winter on the Rocky Mountain Front, with mule deer locations from associated season.

3.2 Multi-scale tradeoffs between forage and risk by migrant and resident mule deer

Partial migration, a phenomenon in which some individuals in a population migrate and others remain resident in the same range year-round (Chapman et al. 2011), is common in mule deer populations. Unlike most ungulates, however, individual mule deer show very little plasticity in whether or where they migrate on an annual basis (Sawyer et al. 2019). Therefore, mule deer may be less resilient to environmental change than more behaviorally plastic species like elk (*Cervus canadensis*; White et al. 1987, Brown 1992, Eggeman et al. 2016, Barker et al. 2019, Sawyer et al. 2019). Mule deer populations have declined throughout their range over the past 3 decades (Monteith et al. 2014), so conservation of habitat on their existing seasonal ranges is particularly important for the long-term viability of declining populations. Understanding resource selection by partially migratory mule deer is important because it could indicate how partial migration is maintained in an ungulate where individual migratory strategies are relatively fixed, and could indicate which resources should be prioritized for conservation of habitat for mule deer (Rettie and Messier 2000, Gaillard et al. 2010).

Accessing high-quality forage during summer is critical for mule deer because it strongly influences over-winter survival (Hurley et al. 2014). Predation risk can also affect mule deer populations indirectly by affecting their behavior, preventing access to high quality foraging areas and exacerbating the effects of decreased foraging opportunities (Atwood et al. 2009, Dwinnell et al. 2019). Within the Northern Rockies of the United States, wolves (*Canis lupus*) and mountain lions (*Puma concolor*) have undergone range expansion and population growth concurrently with changes in forage availability and mule deer declines (Russell et al. 2012, Robinson et al. 2014, Proffitt et al. 2015, Montana Fish Wildlife and Parks 2018a, b). To assess how forage and predation risk influence mule deer behavior, habitat selection should be assessed at multiple spatial scales to reveal behaviors aimed at acquiring food or avoiding predators (Boyce 2006). Whether an individual does or does not migrate can influence how much forage is available to it at broad spatial scales (Dingle and Drake 2007) which can influence how forage is selected and predators are avoided at finer scales (e.g. the home range [2nd order] and within-home range [3rd order] scales; Johnson 1980; Mysterud and Ims 1998, Hebblewhite and Merrill 2009).

We assessed how forage and predation risk conditions differed between migrant and resident mule deer summer ranges. To do this, we used vegetation data from our summer field sampling and developed resource selection functions (RSFs) for wolves and mountain lions to estimate the spatial distribution of predation risk. Then, we assessed how forage and predation risk influenced habitat selection by migrant and resident mule deer during summer by developing RSFs at the 2nd and 3rd order. We used a Bayesian framework and computed coefficients for each individual deer, each migratory strategy by study area, and the average of each migratory strategy. Further, we assessed how ecological context influenced how migrants and residents selected forage and predation risk by evaluating how 2nd and 3rd order selection for those factors varied across a spectrum of forage availability levels.

Forage availability did not vary predictably between migrant and resident summer ranges. Residents had higher forage available to them on the Rocky Mountain Front and Cabinet-Salish, but lower forage in the Whitefish Range (Table 4). Wolf and mountain lion predation risk was similar for migrants and residents in the Cabinet-Salish and Whitefish Range. On the Rocky

Mountain Front, however, migrants faced 26% lower wolf predation risk and 32% higher lion predation risk than residents.

Table 4. Mean availability of forage (kilocalories/square meter) and values from wolf and mountain lion resource selection functions (RSFs; percentile scale) within summer ranges of migrant and resident mule deer in 3 study areas throughout western Montana, with associated 95% credible intervals. "Mig - Res" is the difference between variable means in migrant and resident summer ranges, by study area, with associated credible intervals, and "Prob > 0" is the probability that migrant means are greater than resident means.

Variable	Study area	Strategy	Mean	2.50%	97.50%	Mig - Res	2.50%	97.50%	Prob > 0
Forage	CAB	Mig	3.311	2.612	4.088	-1.318	-2.657	-0.059	0.02
		Res	4.629	3.61	5.767				
	RMF	Mig	4.134	3.286	5.08	-1.347	-3.156	0.332	0.059
		Res	5.481	4.081	7.067				
	WHI	Mig	3.551	2.751	4.446	0.873	-0.298	2.068	0.928
		Res	2.677	1.931	3.536				
Wolf	CAB	Mig	53.75	48.299	59.191	2.996	-4.706	10.798	0.771
		Res	50.76	45.281	56.154				
	RMF	Mig	34.3	28.752	39.74	-25.522	-33.38	1.764	0
		Res	59.83	54.27	65.293				
	WHI	Mig	51.98	46.476	57.504	-2.679	-10.49	5.065	0.251
		Res	54.66	49.121	60.179				
Lion	CAB	Mig	56.69	51.394	62.041	7.644	0.172	15.14	0.977
		Res	49.04	43.612	54.402				
	RMF	Mig	64.72	59.374	70.068	31.96	24.471	39.494	1
		Res	32.76	27.485	38.101				
	WHI	Mig	52.2	46.868	57.632	-3.617	-11.12	3.909	0.174
		Res	55.82	50.455	61.186				

The average behaviors of migrants and residents across study areas were similar. On average, both migrants and residents avoided forage at the 2nd order and selected forage at the 3rd order, avoided mountain lions at the 2nd and 3rd order, and were neutral to wolves at the 2nd order but avoided wolves at the 3rd order (Figure 12). Mule deer generally did not avoid wolves when selecting home ranges, perhaps due to the lower lethality of wolves versus mountain lions we documented. Out of 26 predator-caused mule deer mortalities in our study, 21 were caused by mountain lions, 4 by wolves, and 1 by coyotes. The influence of the apparently more lethal predator (mountain lions) on home range selection may have overridden the influence of the less lethal predator (wolves), which is a common behavioral response of prey in multi-predator systems (Relyea 2003, Morosinotto et al. 2010, Kohl et al. 2019). Selection for forage at the 3rd order.

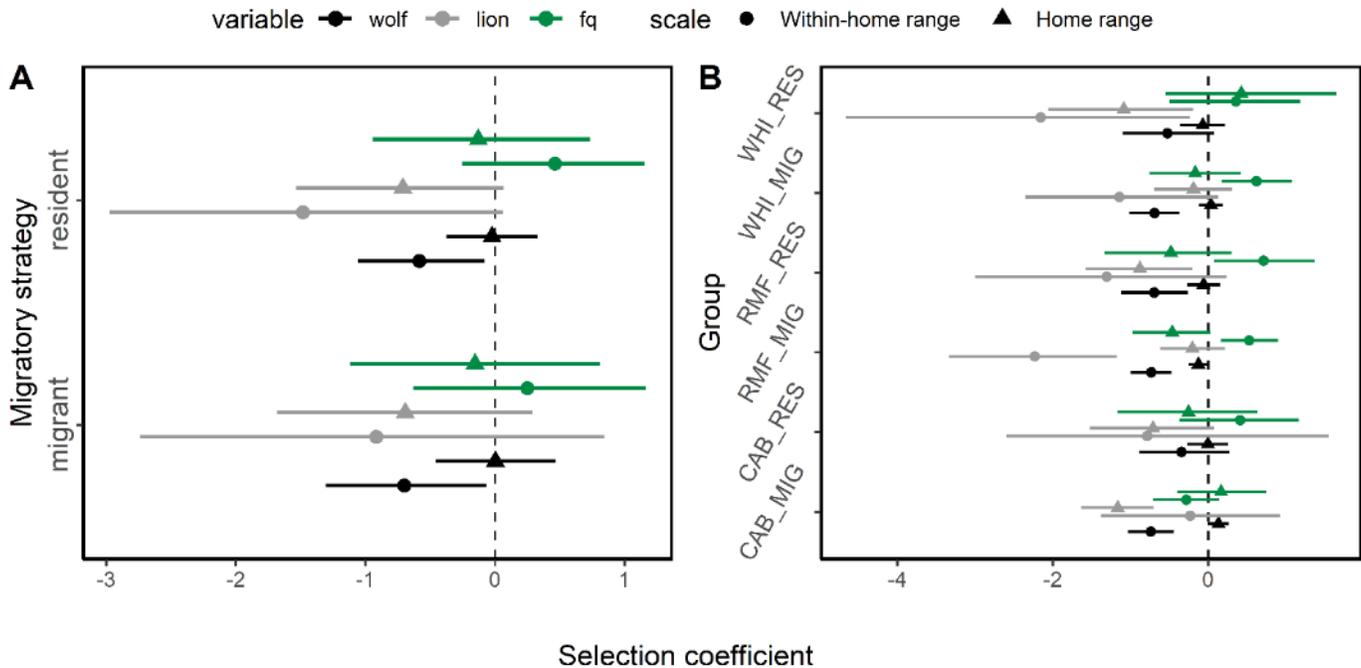


Figure 12. Centered and scaled selection coefficients and 95% credible intervals from Bayesian hierarchical resource selection functions (RSFs). Parameters for predation risk (“wolf” and “lion”) and forage quality (“fq”) were computed at multiple grouping levels including (A) specific migratory strategies and (B) groups of mule deer in each study area by migratory strategy. Y-axis labels in plot B refer to study area and migratory strategy (‘CAB’: Cabinet-Salish, ‘RMF’: Rocky Mtn. Front, ‘WHL’: Whitefish, ‘mig’: migrant, ‘res’: residents).

Across all study areas, the average behavior of both migrants and residents was to avoid forage at the 2nd order. However, there was substantial variation in 2nd order selection for forage among different study areas and strategies (Figure 12, which appeared driven by differences in broad scale forage availability. As landscape-level forage availability increased among groups of mule deer, 2nd order selection for forage decreased (Figure 13). Therefore, the 2 groups with the least forage available to them at broad scales (Whitefish Range residents and Cabinet-Salish migrants) selected forage at the 2nd order. At the 3rd order, the average behavior of migrants and residents was to select for forage, perhaps because mule deer can better perceive forage availability at this scale (Battin 2004). This general behavior held true across all groups of deer, except for migrants in the Cabinet-Salish who avoided forage at the 3rd order.

Given their low plasticity in summer home range selection, and the importance of selecting high quality forage within-home ranges, habitat treatments that improve forage quality and reduce predation risk from mountain lions within summer home ranges may be an effective means of improving mule deer habitat. This could be especially effective in declining populations with a high proportion of migrants. Wildlife managers in Western Montana could use our 2nd order RSFs to identify where mule deer home ranges are likely to be, which could indicate where habitat treatments should take place. Treatments like timber harvests, thins, and wildfires may improve forage quality and reduce hiding cover used by mountain lions within summer home ranges of mule deer.

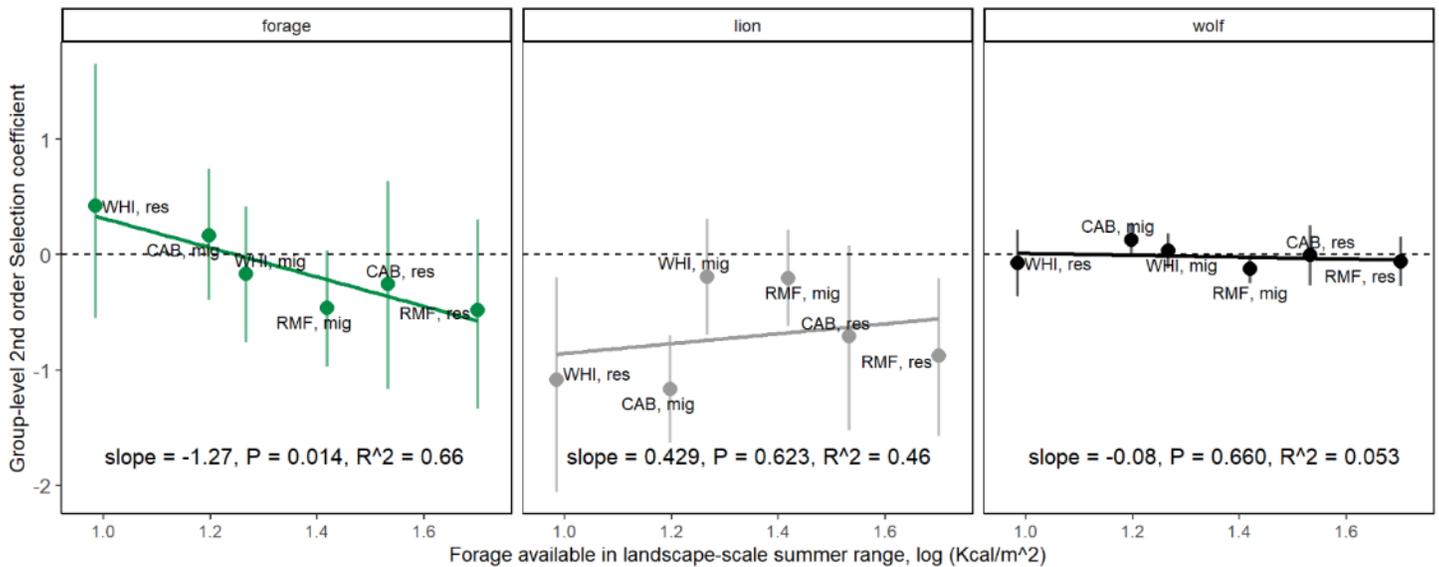


Figure 13. Centered and scaled group-level selection coefficients from 2nd order resource selection functions (RSFs) plotted against mean forage quality (log-transformed) available in landscape-scale migrant or resident summer ranges, labeled by group ('CAB': Cabinet-Salish, 'RMF': Rocky Mtn. Front, 'WHI': Whitefish, 'mig': migrant, 'res': residents).

3.3. Summer responses to landscape disturbance

Across forested ecosystems of Montana, disturbance is an important driver of landscape heterogeneity and the distribution of nutritional resources. Disturbances alter the characteristics and configuration of the nutritional landscape in space by altering forest structure and reducing canopy cover of mature trees. With increasing time since disturbance, forest succession typically results in decreased light and reduced forage biomass for deer in the understory. Anthropogenic disturbance has increasingly replaced wildfire disturbance in the western U.S. (Frelich 2002), and wildfires differ from timber harvests in their effects on understory vegetation and forage. Here, we studied the effects of both anthropogenic- and wildfire-induced disturbances on 1) plant community responses, with specific attention to mule deer forage species, and 2) mule deer behavioral responses. Here, we focus specifically on results for (1) above.

Our assessment of the effects of disturbance on plant communities was founded on multiple metrics of the plant community response. Similar to above, we quantified variation in the available forage nutrition, in both biomass and energy per unit area, as one response metric. However, we also considered other metrics of plant community response, such as overall habitat condition, measured with the floristic quality assessment index (FQAI) and individual responses of important plant species, including both forage species and notable invasive species.

The prevalence of disturbance regimes varied across our 3 study areas, such that wildfire was the dominant disturbance in type in one study area (Rocky Mountain Front) while timber harvest was more prevalent in the Cabinet-Salish study area (Figure 14).

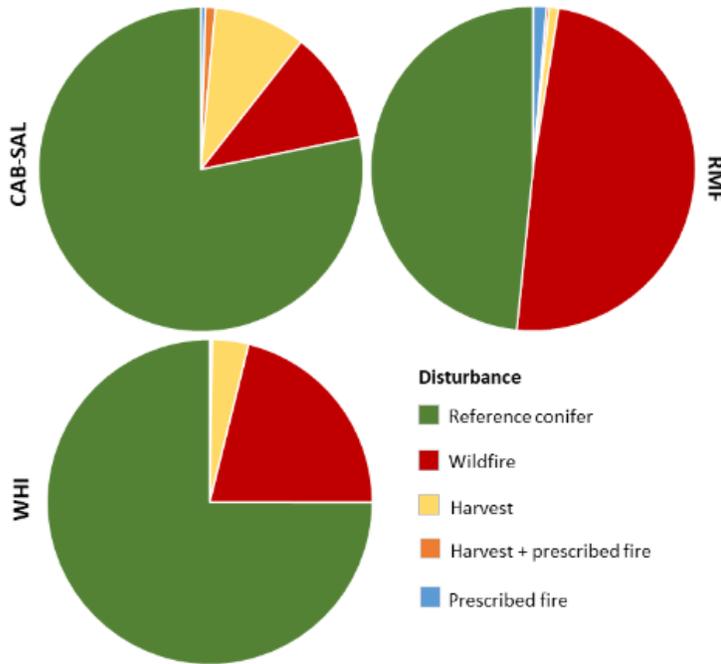


Figure 14. Proportion of disturbance within home ranges of mule deer calculated from 95% kernel density estimates (KDE) of GPS radiocollar locations during summer 2017 – 2019.

We found a high degree variation in how disturbance affected the presence of various forage species (Figure 15). Disturbance type (e.g., wildfire vs. timber harvest) caused varied responses in plant communities, and those disturbance-specific responses also appeared to vary by study area. Despite all this variation, there were some general patterns. Some forage species, such as *Ceanothus*, *Chamerion angustifolium*, *Ribes*, or *Salix* spp. appeared to consistently increase with wildfires, while others such as *Amelanchier alnifolia* and *Rosa* spp. appeared to consistently decrease across all study areas (Figure 15). Responses to timber harvest included generally increased prevalence of species such as *Amelanchier alnifolia*, *Fragaria* spp., and *Ribes* spp. across all study areas, but variable responses of other species, such as *Rubus* spp. or *Spirea betulifolia* (Figure 15).

Land managers are tasked with managing plant communities towards a multitude of end-goals, which might include increased mule deer forage, but also decreased invasive species, increased species richness, increased habitat condition, etc... For this reason, we modeled multiple metrics of vegetation response as a function of disturbance, and then built these responses into a decision analysis. This decision analysis compares and contrasts the various costs-benefits of each management scenario as a function of multiple plant community metrics. We will provide a complete depiction of this analysis in the final study report.

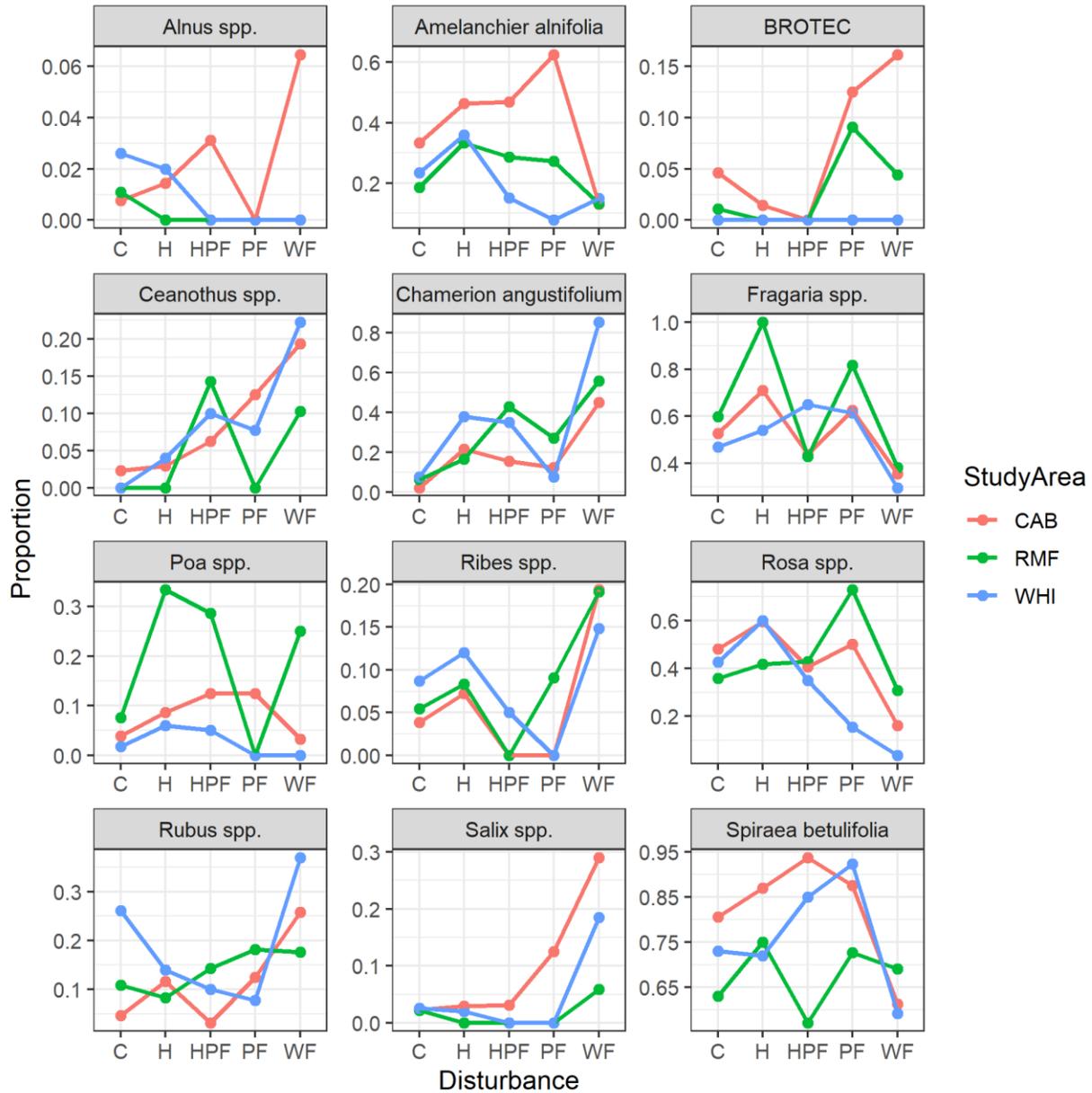


Figure 15. Proportion of vegetation points where top species from mule deer diets were recorded in reference conifer forest (C) and 4 disturbance types: harvest (H), harvest + prescribed fire (HPF), prescribed fire (PF), and wildfire (WF). Species occurrence was from 683 forest vegetation surveys during 2017–2019 in three study areas: the Rocky Mountain Front, the Cabinet-Salish Mountains, and the Whitefish Range.

Objective #4. *Winter mule deer habitat selection*

The winter season produces considerable challenges for ungulates in northwest Montana, including challenges relating to changes in climatic conditions and plant nutritional senescence. While year round strategies are employed during winter like balancing the trade-off between maximizing access to high quality forage against minimizing exposure to the risk of predation, the dramatic change in climatic conditions introduces significant challenges for deer adapting strategies for conserving energy on a changing landscape (Houston et al. 1993, Gilbert et al. 2017). With this in mind, we are currently investigating what drives mule deer habitat selection in winter and how these patterns may differ from previous results on summer habitat selection (Hayes 2020, Peterson 2020). We have developed four competing hypotheses that may explain winter habitat selection and built RSFs using only GPS locations from December 4 to April 28, excluding any locations occurring during an animal's migration. The first hypothesis acknowledges the diverse ecological community of northwest Montana that supports the full suite of native large carnivores and multiple large ungulate species. Further, building off Peterson (2020) we expected the risk of cougar predation to be a driver of habitat use in winter whereby mule deer avoid areas cougars are more likely to exist (Kohl et al. 2019). To test this, we will incorporate an existing cougar RSF developed by Robinson et al. (2015) as a spatial covariate in our mule deer RSF.

Our second hypothesis recognizes that forage quality can have dramatic impacts on ungulate survival and reproductive success (Forrester and Whittmer 2013, Proffitt et al. 2015), thus influencing spatial patterns in habitat use (Nicholson et al. 1997). We will incorporate the aforementioned spatial forage quality model outlined in section 3.1 into our RSF to test if mule deer spatial use patterns can be explained by spatial variation in forage quality. Further, the synergistic impacts of predation and forage availability are likely mediated by variations in climatic conditions (Hopcraft et al. 2010).

Given the significant energy allocation animal's require to maintain constant body temperatures, our third hypothesis predicts that thermoregulation during the frigid winter months will guide mule deer to use areas of the landscape with greater solar radiation and heat saving capacity (Parker et al. 1984a, Cook et al. 2004, Serrouya and D'Eon 2008, Withers et al. 2016). Models addressing this hypothesis included spatial layers of solar radiation that account for topography.

Further, extensive snow accumulation can impede efficient travel or hinder mule deer's ability to easily access forage (Gilbert et al. 1970, Parker et al. 1984b, Fancy and White 1987, White et al. 2009). Nonetheless, high quality forage may outweigh the energetic consequences of travel in deep snow leading to interactive effects of these variables. Our fourth hypothesis suggests that mule deer make habitat selection decisions in order to avoid areas with deep snow. To test this, we will include a measure of snow water equivalence (SWE), which is highly correlated to snow depth, from the SNODAS dataset (National Operational Hydrologic Remote Sensing Center 2004).

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